Worker Versus Sexual, and Sex Ratio Investments in the Social Wasp *Vespula vulgaris* (L.) (Hymenoptera: Vespinae) in England

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Abstract.—An attempt has been made to quantify the relative investment in workers versus sexuals, and queens versus males in *Vespula vulgaris* (L.). In particular I have investigated MacNair's hypothesis that the queen invests equally in queen and male eggs, and that her investment stops after she has laid her eggs. The dry weights and calorific values of the workers, autumn queens, and small-cell, and large-cell, reared males were determined. The lipid content of the autumn queens was 39.9%, and the crop-solid of males was 34.5%, of their dry weight. The seasonal change in worker dry weight was related to the varying work loads of the workers. A simulation model using the compartmental system approach was used to estimate the number of workers, queens and males produced by a successful colony. Investment in workers, either as dry weight or calorific equivalent units, represented nearly 50% of the total colony investment. This is considered a relatively high investment and can be related to the delay of sexual production. Males and queens are produced in about equal numbers but, in terms of dry weight or calorific equivalent units, there is a bias toward queen production. Workers were found to be selectively destroying male brood probably derived from queen eggs. MacNair's hypothesis could not be supported.

In England the annual life-history of *Vespula vulgaris* (Linn.) starts with the emergence of the males and new queens from the mature colonies in the autumn. The sexuals remain in the colonies for a few days before leaving on their mating flights. After a short time the fertilised queens enter over-wintering sites while the males die. When the queens emerge in the spring they each search for a nest site, build a queen-nest and, by early June, rear the first workers. The workers take over the jobs of building the nest and looking after the brood from the queen which continues to lay eggs. At first, the workers build small cells (small-cell colony) in which more workers and, later, males are reared. From the beginning of August, the workers build large cells (large-cell colony) in which the queens and sometimes males are reared. The colony with its queen and workers usually dies by the end of October or early November (Archer 1981a, 1984).

With the emergence of the new queens, brood in the small cells is neglected and not well fed (Montagner 1966). The neglected larvae and sealed brood are frequently pulled out of their cells by the workers and dropped some distance from the nest. This destruction of brood has been frequently recorded (Duncan 1939, Spradbery 1973, Archer 1981a, Greene 1991). The neglected brood also are eaten by dipterous larvae, e.g. *Volucella* sp. (Archer 1981a).

The above life-history in which the reproductive females fly away from their natal colonies and found new colonies independently is called 'Alate Dispersing' (Nonacs 1993). All alate dispersing colonies must make two investment decisions. The first is concerned with the proportion of resources devoted either to the produc-

tion of the workers or to the sexuals. The second is concerned with the proportion of resources devoted to either male or queen production (Nonacs 1993).

The first decision is a process of maximising sexual production. Sexual production could be delayed by the production of more workers for colony maintenance with the trade-off consequence of ensuring a greater future sexual production. Brian (1965) produced a general model of colonial growth which showed that queen production increases with increased investment in workers. Pamilo (1991) developed models for perennial colonies, finding that greater investment in worker production was related to a smaller chance of queens founding new colonies and the old colonies surviving. With the annual colonies of *V. vulgaris*, the old colonies do not survive and the queens have a very small chance of founding new colonies (Archer 1984) so worker production relative to sexual production should be higher. The timing of the switch from worker to sexual production varies between the species of vespine social wasps (Archer 1980, 1981a).

The second decision concerning proportional investments in males and queens focuses on the queen-worker conflict due to asymmetrical genetical relationships (Trivers and Hare 1976, Benford 1978, MacNair 1978, Nonacs 1986, Boomsma 1989, Ratnieks and Reeve 1992). A wide range of variation in sex investment ratios has been found (Crozier and Pamilo 1996), often due to multiple mating by queens and worker reproduction in queenright colonies (Trivers and Hare 1976, Benford 1978).

Usually sex ratio investment is measured by determining the dry weight production of queens and males (Trivers and Hare 1976, Crozier and Pamilo 1996). In a vespine colony with a singly-mated queen and no worker reproduction, it is expected that queens will adjust the sex ratio investment to give equal dry weights of queens and males. Workers, because of

asymmetrical genetical relationships, will increase the investments in queens to three times that of males. If the queen has mated with more than one male and/or there is worker reproduction, the sex ratio investment of the queen is unchanged, but the workers will increase their investment in the males, although investment in queens will still be greater.

MacNair (1978) argued that queen investment stops after the eggs are laid: further investment then is carried out by the workers. Thus the queen should distribute her parental investment equally between queen and male eggs to produce a primary sex ratio of 1:1. For workers to skew the investment towards queens, they should try to prevent the queen from laying male eggs or destroy the brood derived from the male eggs of the queen.

The queens have larger bodies in which to carry sufficient fat bodies to enable them to over-winter. The males do not over-winter but die soon after mating, or attempting to mate, for which purpose a smaller body seems adequate. Thus the departure from equal investment in queen and male eggs by the queen to a relatively greater queen investment does not necessarily imply the workers have succeeded in altering the sex ratio investment of the queen. To demonstrate that workers have succeeded in producing a relatively greater investment in queens, it is necessary to show that male brood derived from queen eggs have been destroyed.

Ideally, the determination of worker and sexual production should be carried out directly by visual observations on colonies under natural conditions. This is difficult to achieve since colonies of *V. vulgaris* are surrounded by envelopes, are often underground, and the workers are aggressive when disturbed during investigations. Visual observations on healthy colonies maintained in an observation box have so far been restricted to one comb, the lowest comb of the nest (Potter 1964).

However, indirect methods can be used

to estimate the production of workers and sexuals. Colonies can be collected throughout the year and counts made of the brood and adults present. At the end of the last larval stage the gut contents are evacuated to form the black meconium at the bottom of the cell. Counts of these meconia can be used as an estimate of the number of adults reared. Since a meconium is only evidence that a larva has pupated, the result could be an over-estimate if incipient adults died during the pupal stage. In addition, the meconial remains do not reveal the sex or caste of the former occupants of the cells. Thus precise counts of worker and sexual production cannot be made from collected colonies, although counts of meconia and queen and male sealed brood can give a first approximation (Archer 1993).

To improve the accuracy of estimating worker and sexual production a simulation model of a successful colony, i.e. one that rears many queens, has been developed (Archer 1981a, 1981b). The simulation model not only used the data from 198 collected colonies of *V. vulgaris* but also laboratory observations on the length of life of the brood stages and adult workers. The model incorporates meconial information for adult production, and rates of cell building, brood stage addition and adult appearance estimated from the collected data. Brood neglect and mortality were incorporated into the model to come into effect when adult and brood stages became too numerous in comparison with the data from collected colonies. The model achieves greater realism at the expense of complexity, with the use of 253 parameters and variables. To handle such a complex model the compartmental system approach (Odum 1971) was used.

In this paper, I will try to determine the extent of any destruction of queen-derived male brood to test the proposal of MacNair (1978), and derive estimates of the production of workers, males and queens to determine the relative importance of

worker production, and the relative investment in males and queens.

METHODS

Sources of, and treatment of workers.—Workers were bait-trapped during 1970 at Averhams Plantation, between Flaxton and Claxton, about 12 kilometres to the north-east of York, England. Averhams Plantation was an open site with a dense herb layer and recently planted conifers. The trapping station consisted of 16 sub-stations arranged in a square (4×4) with two traps at each sub-station. The traps were attached to canes about 70cm above the ground. Each trap consisted of a white polythene container (75mm deep, 75mm diameter) with a 10mm diameter hole in the lid, and contained a jam solution with added yeast. The fermenting jam solution was changed once every two weeks and the catch of workers collected once a week. Trapping was continuous from July until October. The workers were preserved in 70% ethanol.

Samples of 50 workers from each weekly catch were dried to constant weight in an air oven at 60°C. During July and October when the number of workers trapped were smaller all workers were dried. Each weekly sample of dried workers was weighed to 0.1mg. The weekly dry weight was divided by the number of workers in the sample to give the mean worker dry weight.

Workers from seven colonies were collected during late June and preserved by deep-freezing. Later the dry weights of these workers were obtained as previously described except that workers were weighed individually so a standard deviation could be calculated.

Correction for dry weight of workers due to 70% ethanol preservation.—To determine if ethanol-preserved workers lost dry weight, samples of 50 or 55 workers from three colonies were preserved in 70% ethanol and by deep-freezing. After about six months of such preservation dry weights

were obtained as previously described. Ethanol preserved workers showed a loss of dry weight compared with deep-frozen preserved workers from all three colonies. The percentage dry weight loss was 20.5%.

Sources of, and treatment of queens.—Autumn queens with fully developed fat bodies were collected from four colonies. From three colonies 172 queens were preserved by deep-freezing and from one colony 47 queens were preserved in 70% ethanol. Dry weights were obtained as previously described for workers except that queens were weighed individually. Dry weight loss from ethanol preservation was found to be 11.4% based on queens collected from one colony when 55 queens were preserved in 70% ethanol and 63 by deep-freezing.

Sources of, and treatment of males.—Males with full crops were collected from a colony which was rearing males both in the small and large cells. All 102 males were preserved in 70% ethanol. Dry weights were obtained as previously described for workers except that males were weighed individually. The dry weights of the males showed a bimodal distribution indicating a weight difference between males reared in the small and large cells. A method given by Lewis and Taylor (1967) was used to separate the 56 small-cell and 46 large-cell reared males.

Males with full crops were collected from three colonies which had reared males only in the small cells. From the three colonies 146 males were preserved by deep-freezing. Dry weights were obtained as previously described for workers except that males were weighed individually.

Dry weight loss from ethanol preservation was found to be 37.7% based on males collected from three colonies when 201 males were preserved in 70% ethanol and 146 by deep-freezing.

Lipid determinations.—Samples of workers, autumn queens and males were pre-served by deep freezing and extracted in the Soxhlet apparatus using trichlorethylene as a solvent. Extraction was continued until constant weight was obtained. Nine queens were extracted individually, 27 males in batches of threes, and 74 workers from three colonies in colony batches.

Male crop content determinations.—When males left their natal colonies in the autumn their crops were found to contain a clear viscous fluid. From one colony 50 males were collected and preserved by deep freezing. Their crop fluid was collected by cutting the gaster away from the rest of the body and gently squeezing the gaster so that the crop fluid could be absorbed by a known dry weight of filter paper. The filter paper with its absorbed crop fluids were dried in an air oven at 60°C to constant weight. All weightings were made to 0.1mg. Some general biochemical tests were performed on the crop fluid.

Ash content of workers, autumn queens and males.—A sample of 22 autumn queens was collected, preserved by deep-freezing, and dried by freeze-drying. Samples of 74 workers and 27 males were obtained from the lipid-extracted individuals. The samples were heated in a furnace at 500°C for three hours and the residue ash weighed to 0.1mg.

Calorific determinations.—Samples of workers, autumn queens with fat bodies and males with full crops were preserved by deep freezing, dried by freeze-drying and their calorific values determined with the aid of a Phillipson Oxygen Microbomb Calorimeter (Phillipson 1964).

Due to the high lipid content of the autumn queens oil was lost when the animal tissue was pelleted in preparation for bomb calorimetry. Attempts to bomb nonpelleted material as suggested by Woodland *et al.* (1968) and Howell and Fisher (1977) failed because oil was lost from the sample and found at the bottom of the bomb. The lipids were extracted, as pre-
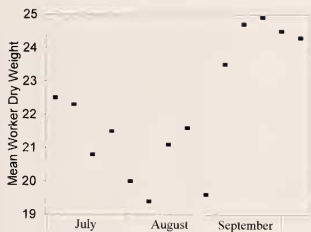
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July   August   September

Fig. 1. Mean worker dry weight (mg) versus date for *Vespula vulgaris*.

Mean Worker Dry Weight

Table 1. The mean dry weights of workers of *Vespula vulgaris* from late July colonies.

Date	No. workers	Mean dry weight (mg)	Standard deviation
17	13	25.1	3.93
20	14	22.0	4.11
29	33	21.2	5.24
30	15	24.6	5.59
30	34	21.9	5.09
30	35	24.4	5.66

viously described, and the calorific determinations made on the remaining tissues.

Difficulties sometimes were experienced when freeze-drying males in that the viscous contents of the crops would not freeze-dry but rather exploded out of the male into the freeze-drying equipment. Calorific determinations were made on crop-extracted males, as previously described, and on males with crop fluids where freeze-drying was satisfactorily completed.

Simulation model of colonial determination.—The development of a simulation model is given in Archer (1981a). The model was developed on the DEC system-10 computer at the University of York, England. Recently the model has been transferred to a Personal Computer.

RESULTS

Seasonal variation of worker weights.—The seasonal change in the dry weights of workers from the bait traps is shown in Fig. 1. These dry weights have been corrected for dry weight loss during ethanol preservation. From a high mean dry weight during early July there is a decrease to a low value during August, followed by an increase during the first half of September, after which there is a slight decrease during late September and October.

The mean dry weights of the workers from the late June colonies are given in Table 1. The mean dry weight from the seven colonies is 23.3mg which is slightly higher than the value for early July (Fig. 1).

Lipid content of workers, autumn queens and males.—The lipid content of the workers is given in Table 2. The higher lipid content corresponds with the higher mean dry body weight found during September.

The mean lipid content of a male was 7.4mg (range 4.1–9.1) representing 10.3% of the mean dry body weight.

The mean lipid content of a queen was 65.0mg (s.d. 8.2) representing 39.9% of the mean dry body weight.

Male crop fluid.—The mean dry weight of the crop fluid was 32.3mg (s.d. 9.98) which represented 60.5% of the wet weight of the crop fluid. The mean dry weight of the crop fluid represented 34.5% of the mean dry body weight. The dry weight of the crop fluid of each male was positively correlated with its dry body weight (n = 50, r = 0.57, p < 0.001).

The crop fluid gave a positive result with two general carbohydrate tests: (a)

Table 2. The lipid content of adult workers of *Vespula vulgaris*.

Date	No. workers	Lipid extracted (mg)	% lipid of dry body weight
20 Jul.	20	23.0	5.7
26 Aug.	25	16.7	3.1
23 Sep.	29	95.5	10.1

Table 3. The mean dry weight of autumn queens of *Vespula vulgaris*.

Date	No. queens	Mean dry weight (mg)	Standard deviation
12 Sep.	22	163.7	11.18
20 Sep.	47	167.1*	11.75
9 Oct.	59	167.6	10.43
31 Oct.	91	155.3	8.43

* Corrected for 70% ethanol preservation.

Table 4. The mean dry weight of small-cell reared males of *Vespula vulgaris*.

Date	No. males	Mean dry weight (mg)	Standard deviation
12 Sep.	50	81.1	14.3
16 Sep.	56	87.3*	14.7
23 Sep.	50	96.3	23.0
31 Oct.	46	74.0	13.9

* Corrected for 70% ethanol preservation.

alcoholic thymol and conc. hydrochloric acid and (b) alcoholic alpha-naphol and concentrated sulphuric acid. A positive reaction also was obtained with Benedict's reagent indicating the presence of reducing sugar.

Queen dry weight.—The mean dry weights of autumn queens with fat bodies are given in Table 3. The closeness of the deep-freeze and corrected ethanol-preserved queens gives confidence in the use of the correction factor. The mean of the four samples is 163.4mg. Since these autumn queens consisted of 39.9% lipid content the mean dry weight would be made up 65.2mg lipid and 98.2mg non-lipid substances. The dry weight of lipid of each queen was positively correlated with its dry body weight (n = 19, r = 0.79, p < 0.0001).

Male dry weight.—The mean dry weights of males reared in the small cells are given in Table 4. The closeness of the deep-freeze and corrected ethanol-preserved males gives confidence in the use of the correction factor. The dry weight of the four samples is 84.7mg. Since the crop solid consisted of 34.5% of the body dry weight, the mean dry weight would be made up of 29.2mg crop solid and 55.5mg for the rest of the body.

The mean dry weight of males reared in large cells was 130.7mg. This dry weight has been corrected for dry weight loss during ethanol preservation. Assuming 34.5% of this dry weight was crop solid, the mean dry weight would be made up

of 45.1mg crop solid and 85.6mg for rest of the body.

Calorific determinations.—The ash content of the adults was so low that it was unlikely to complicate the calorific determination. The ash percentage of mean dry weight for autumn queens was 2.8%, for males 2.9% and for workers 2.5%.

The mean calorific values of lipid-extracted queens, males and workers are given in Table 5. Assuming the calorific equivalent of queen lipid to be 9.2 cal/mg (Sawicka-Kapusta 1975) and knowing the lipid percentage of mean dry body weight then the calorific value of the total dry body weight of the queen would be 6.627 cal/mg dry weight.

Knowing the mean calorific values of crop-extracted males and males with crops (Table 5), it can be calculated that the crop solid has a calorific value of 4.232 cal/mg dry weight. Such a calorific value indicates that the crop solid was a protein or carbohydrate rather than a lipid substance. Earlier results showed that the

Table 5. Calorific values of autumn queens, males and workers of *Vespula vulgaris*.

	Sample size	Cal/mg dry weight	Standard deviation
Queen (lipid extracted)	10	4.820	0.085
Male (crop extracted)	10	5.201	0.149
Male (with crop)	10	4.872	0.142
Worker — 17 Jun.	10	5.092	0.122
Worker — 28 Jul.	10	5.273	0.147
Worker — 24 Sep.	10	5.220	0.109
Worker — combined	30	5.195	0.145

Table 6. The number, biomass (dry weight) and calorific equivalent of queens, queen lipid, males, male crop content and workers produced in a simulation colony of *Vespula vulgaris*.

	Number	Biomass (mg)	Calorific equivalent (cal)
Workers	10,248	217,072.3	1,127,690.6
Males			
Small cells	763	64,626.1	314,858.4
Large cells	261	34,112.7	166,197.1
Total	1,024	98,738.8	481,055.5
Crop solids		34,064.9	144,162.6
Queens	969	158,334.6	1,049,283.4
Lipid		62,985.0	579,462.0
Total	12,241	474,145.7	2,658,029.5

Table 7. The dry weights of workers of *Vespula vulgaris* during the seasonal development of a colony derived from Fig. 1 and Spradbery (1972).

Date	Dry weight (mg)
6 Jun.	11.75 (Spradbery)
16 Jun.	11.75 (Spradbery)
6 Jul.	22.4
11 Aug.	19.5
14 Sep.	24.9
5 Oct.	24.3

crop solid is a carbohydrate, probably reducing sugar.

Since the calorific values of workers varies little from samples collected during June, July and September a combined value has been calculated (Table 5).

The mean calorific values for workers and crop-extracted males are similar, but less than the mean calorific value of autumn queens because of the high lipid content of queens. The low mean calorific value of males is due to the high carbohydrate content of the crop. The lipid-extracted queens have a lower mean calorific value than the workers and crop-extracted males, as these workers and males have some lipid in their bodies.

Production estimates of a successful colony.—The number, biomass and calorific equivalents of the workers, males and queens produced in the simulation model are given in Table 6. The biomass and calorific equivalents of the males and queens were calculated by multiplying the number of males and queens produced by the model by the appropriate mean dry weight and calorific values. The crop solid of the males represents 30.0% of their calorific equivalent and the lipid of the queens 55.2% of their calorific equivalent.

Since the dry weight of workers varies during the development of the colony

(Fig. 1), it is necessary to know the dry weight of the workers on the days that they emerged as adults. These emergence dry weights were assumed to be those of the collected workers, half the length of worker life before the date on which the workers were collected (Archer 1981a). The model calculated the number of adult workers produced each day which was multiplied by the appropriate mean dry weight derived from Fig. 1 and given in Table 7. Increases and decreases in mean dry weight were assumed to be linear. The total worker dry weight produced could be multiplied by worker mean calorific value to give the total calorific equivalent.

The relative investment in workers, males and queens of a successful colony is given in Table 8. Just over five workers are needed to rear each sexual, but because sexuals are heavier than workers a greater biomass or calorific equivalent of sexuals is produced than for workers. Workers represent 45.8% by dry weight and 42.4% by calorific equivalent of the total production of the colony.

Slightly more males than queens are

Table 8. The relative investment in workers, males and queens in a simulation model of a successful colony of *Vespula vulgaris*.

	Number	Biomass (dry weight)	Calorific equivalent
Sexuals: Workers	1:5.14	1:0.84	1:0.74
Queens: Workers	1:10.58	1:1.37	1:1.07
Queens: Males	1:1.06	1:0.62	1:0.46

reared, but, because queens are heavier and of higher calorific value, the sex ratio investment changes markedly in favour of the queens. Because the males have higher metabolic rates than queens, the energetic cost ratio (Boomsma 1989, Bourke and Franks 1995) can be used. The sex ratio investment then becomes one queen to 0.72 male, still indicating an investment in favour of queens.

DISCUSSION

Worker dry weight.—A similar seasonal change in the dry weight of workers of *V. vulgaris* from early July until October (Fig. 1) was found by Spradbery (1972) in England and by Malham (1996) in New Zealand for the equivalent season. Spradbery (1972) also found a very low worker dry weight during June (Table 7): these were queen-reared workers. Brian and Brian (1952) also found that queen-reared workers of *Dolichovespula sylvestris* (Scopoli) had low weights.

Malham (1996) found that in areas where insecticide had been used to drastically reduce the number of workers, the dry weight of workers during March (equivalent to September in England, Fig. 1) was markedly higher than in untreated areas. This difference was less pronounced earlier in the season and had disappeared by the end of the season. Malham (1996) attributed the difference to food availability. In treated areas, relatively more food would be available per forager, so larvae would receive more food and produce workers of a heavier weight.

The low worker dry weight during August (equivalent to February in New Zealand) varied from 12–13mg (Malham 1996) to 17.4mg (Spradbery 1972) and 19.5mg in the present study. The high worker dry weight during September (equivalent to March in New Zealand) varied from 17–20mg (Malham 1996) to 20.8mg (Spradbery 1972) and 24.9mg in the present study. Following Malham (1996) these variabilities in dry weights could be due

to shortages in food supply as forager density increases.

The variation in worker dry weight also can be related to variation of the work load on workers. The work load will depend on the number of larvae to feed (larva/worker ratio), the number of cells to build, and the amount of soil to be excavated to make the cavity for the nest. Time spent in excavation and building could reduce the time available to feed the larvae.

The low weights of queen-reared workers could be a consequence of very high larvae per queen ratio, up to 30 larvae per queen, and high cell building rates, in excess of two cells per day (Archer, unpublished).

The relatively rapid increase in worker dry weight by late June until early July could be a consequence of workers aiding the queen in brood rearing. At this time the larva/worker ratio rapidly decreases to about 3–4 and the cell building rate to about one cell per worker per day (Archer 1981a).

The decline in worker dry weight from early July until August coincides with the development of the small-cell colony during which a large worker population is reared (Archer 1981a). Workers sampled during August also had the lowest lipid content (Table 2). Despite the exponential growth of the small-cell colony, the work load on workers continues to decrease with larva/worker ratio decreasing to about one, and cell building rate per day per worker approaching zero. However the amount of excavation greatly increases and over 90% of the outgoing workers from a colony may be carrying earth particles (Archer, unpublished).

The increase in dry weight from August until September coincides with the development of the large-cell colony when the future sexuals are reared. Workers sampled during September also had the highest lipid content (Table 2). During this time the worker load remains low. Larva/worker ratio remains at about one, and

large cell building rate per worker per day is very low at about 0.04 (Archer 1981a). Soil excavation continues but usually less than 20% of outgoing foragers are carrying earth particles (Archer, unpublished).

Queen dry weight.—Spradbery (1973) and Harris and Beggs (1995) found that nearly 40% of the dry weight of autumn queens is lipid, which is similar to the value given earlier in this paper. The same authors found that the lipid was used as a food source of which about three-quarters was used during the over-wintering period. By dissecting queens of *Vespa affinis* (Linn.) from southern Japan, Martin (1993) found that the contents of the fat bodies were used up during the over-wintering period of four to five months.

Harris and Beggs (1995) found the mean dry weight of autumn queens from New Zealand was 121.7mg (range 108.0–154.5), which is about 26% lower than the mean weight reported in the current study. They suggested the low weight of autumn queens was because the fat bodies of the queens had not reached their maximum level of lipid storage. The low weight of queens also could be a consequence of the very high colony densities: up to 33 colonies per hectare found in New Zealand, compared with up to about two colonies per hectare in England (Edwards 1980). At lower colony densities relatively more food resources might be available for queen rearing.

Male dry weight.—By measuring the wing length of males of *Vespa crabro* Linn., Potter (1964) also found a bimodal distribution of male size. Measurements were carried out on callow adults found in their cells. He also recorded that males of some colonies of *V. vulgaris* showed a bimodal size distribution but gave no numerical details. Potter's observations support the interpretation of the bimodal size distribution of males presented in this paper.

The carbohydrate food reserve found in the crops of the males seems to be a new observation. The function of this food reserve would be to provide a readily available source of energy needed by the males when flying around their mating circuits (Edwards 1980).

Worker-sexual ratio investment.—Investment in workers represents nearly 50% of the total biomass investment of a colony (Table 8). By reference to Pamilo (1991, Table 2) the investment in the workers can be considered to be relatively high. This large investment in workers can be related to the delay of sexual production until September in *V. vulgaris*, with the consequence of a larger output of queens (Brian 1983). Sexual production in *Dolichovespula sylvestris* (Scopoli) occurs earlier, during July, so this species has a relatively smaller investment in workers, and also a smaller output of queens (Edwards 1980).

Sex ratio investment.—The more-or-less equal production of queens and males in *V. vulgaris* (Table 8) seems rather surprising since at the sealed brood stage, the number of males is usually twice the number of queens (Archer 1981a, Greene 1991). However, Archer (1981b) found that 45% of large-cell male sealed brood was destroyed, and observed large-cell male sealed brood and mature larvae were carried away from the colonies by the workers. If these large-cell sealed brood are included in the calculation of the primary sex ratio, the ratio becomes one queen to 1.28 males.

The simulation model allows for this destruction of large-cell larvae and sealed brood, as well as for the neglect and destruction of small-cell larvae and sealed brood. The output of the model indicates that 18.4% small-cell larvae and sealed brood will be neglected and destroyed. Since this destruction occurs in the later part of colonial development, most of the destroyed small-cell brood will be males (Archer 1981a). Thus the primary sex ratio would be even more biased towards the males.

The interpretation of the above observations and calculations would indicate

that the queen is not laying an equal number of male and queen eggs as MacNair (1978) suggested. Since males are smaller than queens, the queen would seem to be laying relatively more male eggs so that the investment in adult queens and males eventually becomes equal.

It is possible that the extra male eggs are derived from the workers and the destruction of the male brood an example of worker policing against male production by other workers (Ratnieks 1988), which is predicted when the queen mates with more than two males. Multiple matings by queens of *V. vulgaris* are highly likely (Page 1986). However, Ross 1986 and Bourke 1988, failed to find evidence of *Vespula* workers laying eggs in queenright colonies.

The workers would appear to be destroying male brood so as to bias investment towards the queens. However the sex-ratio investment does not reach three queens for every male (Table 8) probably because of multiple mating by the queen (Page 1986).

The destruction of males by the workers does not take place until the male brood has reached the mature larval and sealed brood stages. Thus, the queen would seem to be able to disguise the sex of her offspring during the egg and early larval stages. MacNair (1978) proposed that there would be an evolutionary race between the queens and workers, with genes selected which favour the disguise of the sex of the brood, followed by genes which enable the disguise to be penetrated. The evolutionary race seems to have reached an equilibrium with detection occurring at the late larval and sealed brood stages after the workers have made a considerable investment in rearing males.

Brood destruction.—Brood neglect and destruction has been linked to the death or physiological breakdown of the queen, leading to the disintegration of the social life of the colony (Spradbery 1973). However, the queen brood are not neglected but well fed (Montagner 1963), and selective destruction of male brood occurs in the large cells (Archer 1981b).

One consequence of the loss of queen influence is the appearance of a dominance struggle among the workers (Montagner 1966), whose ovaries start developing (Greene 1991). Workers with developed ovaries lay eggs destined to become males, although due to the lateness of the season it is unlikely these males will be reared, or if reared, will successfully mate (Ross 1985). Probably the capacity of workers to rear males from worker eggs is an adaptive response to the premature death or physiological breakdown of the queen (Ross 1985). About 28% of the colonies surviving until at least September (Archer, unpublished) are unsuccessful in producing many queens (Archer 1981b), but nevertheless rear males in the small cells. Many of these males could be derived from worker eggs.

In conclusion the outcomes of the two investment decisions of successful colonies of *V. vulgaris* have been found as follows. The first decision of the trade-off between worker production for colony maintenance and sexual production is to delay sexual production in order to produce more workers and hence to produce relatively more sexuals. In the second decision, there is a bias towards queen production at the expense of male production. This bias depends on worker action in the destruction of male brood probably derived from queen eggs.

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